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Wetland drying linked to variations in snowmelt runoff across Grand Teton and Yellowstone national parks

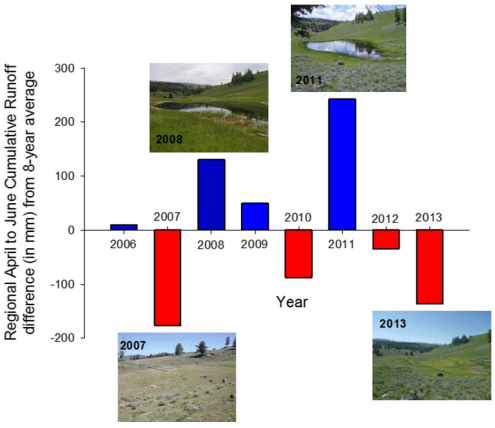
Andrew M. Ray [a,*], Adam J. Sepulveda [b], Kathryn M. Irvine [b], Siri K.C. Wilmoth [b], David P. Thoma [a], Debra A. Patla [c]

[a] National Park Service, Greater Yellowstone Inventory and Monitory Network, 2327 University Way, Suite 2, Bozeman, MT 59715, United States of America
[b] U.S. Geological Survey, Northern Rocky Mountain Science Center, 2327 University Way, Suite 2, Bozeman, MT 59715, United States of America
[c] Northern Rockies Conservation Cooperative, P.O. Box 2705, Jackson, WY 83001, United States of America

HIGHLIGHTS

- In protected areas climate change is the greatest threat to wetland persistence.
- Water balance models provide estimates of the primary drivers of wetland change.
- Temporal and spatial variations in runoff best explained wetland drying.
- Subbasin differences in wetland drying were documented.

GRAPHICAL ABSTRACT



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ABSTRACT

In Grand Teton and Yellowstone national parks wetlands offer critical habitat and play a key role in supporting biological diversity. The shallow depths and small size of many palustrine wetlands in these protected areas and elsewhere make them vulnerable to changes in climate compared with larger and deeper aquatic habitats. Here, we use a simple water balance model to generate estimates of biophysical drivers of wetland change. We then examine the relationship between wetland inundation status and four principal drivers (i.e., temperature, precipitation, evapotranspiration, and runoff) spanning varying meteorological conditions over an 8-year time series from Grand Teton and Yellowstone national parks. We found that models containing snowmelt runoff outperformed models with other meteorological drivers and determined that a higher percentage of surveyed wetlands were dry in years characterized by lower runoff. Our work further shows that wetland drying was widespread across both parks, but sub-regional variations were best described at the hydrologic subbasin-level. Documenting the varying responses of wetlands to meteorological drivers is a necessary first step to identifying which subbasins are most sensitive to recent climatic change and contemplating how future change may alter the distribution of wetlands and their dependent taxa.

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* Corresponding author.
E-mail address: andrew_ray@nps.gov (A.M. Ray).

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1. Introduction

Wetlands are ecosystems of global importance recognized for their rich biodiversity, economic value, and societal services (Junk et al., 2012; Russi et al., 2013). Degradation and loss of wetlands threaten local and regional biodiversity, disrupt water, nutrient, and carbon storage, affect recreational opportunities, and limit the potential for wetlands to contribute to climate regulation (Moomaw et al., 2018). Global declines in wetland habitats have reduced wetland extent by 70% over the last century (Davidson, 2014). More troublingly, an average of 30% decline in wetland area has occurred just over the last four decades (Dixon et al., 2016). Humans have contributed disproportionately to wetland loss by draining, filling, and converting natural wetlands to other land uses (Brinson and Malvárez, 2002). Changes in climate are also linked to contemporary wetland loss (Burkett and Kusler, 2000; Čížková et al., 2013; Desta et al., 2012; Junk et al., 2012; Lee et al., 2015), however, a stronger understanding of the links between changes in climate and wetland drying will be required to direct future conservation planning (Ryan et al., 2014; Sofaer et al., 2016).

In semi-arid regions, the shallow depths, high surface area to volume ratio, and large evapotranspiration water losses make palustrine (i.e., inland, non-flowing) wetlands more vulnerable to changes in climate than deeper aquatic habitats (Matthews, 2010). At higher elevations and in northern latitudes, cooler spring and summer temperatures are associated with greater wetland area and a greater abundance of inundated wetlands (Lee et al., 2015; Sofaer et al., 2016). Conversely, periods marked by warmer temperatures coincide with periods of reduced wetland area and fewer wetlands with standing water (Schook and Cooper, 2014).

Continued warming is projected to alter future inundation patterns of northern latitude, semi-arid palustrine wetlands in multiple ways. First, warmer temperatures will lead to earlier snowmelt runoff, extended ice-free periods, increased evapotranspiration losses, and increased infiltration to dry soils (Johnson et al., 2010; Lee et al., 2015; Matthews, 2010). For all wetlands, increased temperatures are expected to contribute to higher evapotranspiration rates. For deeper wetlands, warmer periods could produce shallower depths and warmer surface waters (Ryan et al., 2014). Shallow, seasonal wetlands may shrink and exhibit an abbreviated hydroperiod relative to historical conditions or be eliminated altogether (Johnson et al., 2010). Widespread drying of shallow wetlands is likely to intensify in semi-arid regions where increased temperatures coincide with reduced precipitation (Cook et al., 2014; McMenamin et al., 2008).

Changes in the timing, form, and magnitude of precipitation are also expected to influence the distribution and persistence of many semi-arid wetlands (Blanken, 2014; Dwire et al., 2018; Schook and Cooper, 2014). In some regions, increased wetland area was historically coupled with multi-year periods of high precipitation and large snowpacks (Halabisky et al., 2016; Johnson et al., 2004; Schook and Cooper, 2014). However, the individual response of a wetland to fluctuations in precipitation, also depends on its connectivity to surface or groundwater and the size of its contributing basin (Dangles et al., 2017; Winter, 2000). If groundwater or surface water (e.g., through riverine contributions) support is high, a wetland may be less responsive to annual or even multi-year changes in precipitation or snowpack compared to hydrologically isolated wetlands (Schook and Cooper, 2014).

Untangling precipitation and temperature effects on the interannual variations in wetland flooding patterns has proven difficult because temperature and precipitation interact with soil and topographic characteristics of contributing basins and with individual wetlands (e.g., shallow versus deep, large versus small, round versus irregular shaped) in complex ways (Dangles et al., 2017; Halabisky et al., 2016; Lee et al., 2015). Moreover, while temperature and precipitation vary seasonally, annually, and on decadal and longer-term scales, changes in temperature also affect the timing, intensity, and form of precipitation (Trenberth, 2011). For an individual wetland, the interactive effects of precipitation and temperature can be conceptualized through a simple water balance approach (Bardecki, 1991).

When increased temperatures are accompanied by increases in precipitation or larger snowpacks, increased precipitation can potentially offset increases in temperature-induced evapotranspiration; the resultant is minimal change in wetland storage or a shifting of the hydroperiod. However, if increased temperatures combine with average or reduced levels of precipitation, declines in wetland storage or shifts to earlier spring flooding and earlier onset of drawdown should be expected (Johnson et al., 2005; Klein et al., 2005; Sorenson et al., 1998). To highlight this point, Johnson et al. (2010) showed that precipitation increases on the order of 5 to 7% above baseline in North America's Prairie Pothole Region (PPR) would be needed to offset each degree of temperature increase. Lastly, the timing of precipitation is also important to wetland flooding dynamics. For example, rain on snow events or a rapid, late winter thaw when the ground is still frozen may contribute less to wetland storage than a slow, spring melt (Mortsch, 1998). Although individual wetlands are expected to respond differently to changes in the magnitude and timing of precipitation and temperature, a growing body of evidence suggests that the changes in temperature rather than precipitation may contribute disproportionately to future wetland drying and more drought-like conditions (Cook et al., 2014; Klein et al., 2005).

Even within the boundaries of protected areas like national parks of the United States (U.S.), resource management may be unable to offer wetlands refuge to the expected effects of climate change. For example, within Olympic and Mount Rainier national parks, climate projections for 2080 suggest fewer wetlands and a shift from permanent and perennial wetland types to ephemeral wetlands (Lee et al., 2015). In the Northern Range of Yellowstone National Park some of these predictions have already been observed. There, wetland area has contracted over the last century (Schook and Cooper, 2014) and a sizable reduction in the number of permanent and ephemeral wetlands was documented in just the last three decades (McMenamin et al., 2008). While future shifts in depth, permanency, and number of wetlands are expected to be widespread, large, climatologically-heterogeneous protected areas may also contain regions where wetlands are buffered from future change (Lee et al., 2015). Such areas, with their portfolio of wetlands types, will become increasingly important to maintain viable populations of wetland dependent species (McCaffery et al., 2014; Ryan et al., 2014).

Here, we use a simple water balance model to generate biophysical drivers of wetland change. We then examine the relationship between wetland inundation status and four important meteorological drivers (i.e., temperature, precipitation, evapotranspiration, and runoff) over an 8-year time series from Grand Teton and Yellowstone national parks. In palustrine wetlands that contain few components, simple water balance models can be used to describe how the individual and interactive changes in meteorological drivers alter the balance of hydrologic inputs and losses from wetlands (Bardecki, 1991; Klein et al., 2005; Winter, 2000). Hydrologic inputs to a wetland water balance include precipitation, surface or overland flows (i.e., runoff), and groundwater inputs. Hydrologic losses are principally associated with evapotranspiration and losses to soil infiltration. Climate change will alter the magnitude and timing of water balance variables as temperature and precipitation interact with site level factors that control how and when water moves through the environment.

Here, we assess the probability of wetland drying from a multi-year (2006 to 2013), spatially diverse monitoring dataset collected across Grand Teton and Yellowstone national parks representing a large, largely intact and climatologically heterogeneous region (Sepulveda et al., 2015; Tercek et al., 2012). Specifically, we used gridded meteorological data and annual in situ observations of wetland flooding status (inundated or dry) to examine whether the probability of wetland drying was associated with spatial and temporal variations in important meteorological drivers that contribute to hydrologic change (Klein

et al., 2005; Lee et al., 2015). We also investigated whether wetland drying probabilities varied among catchments and larger hydrologic subbasins.

2. Materials and methods

2.1. Study area

Grand Teton National Park, John D. Rockefeller, Jr. Memorial Parkway, and Yellowstone National Park (combined area ~10,300 km^2) are adjacent national park units located primarily in northwest Wyoming, U.S.A. (Fig. 1). Hereafter, Grand Teton National Park refers to lands within Grand Teton National Park and the adjacent John D. Rockefeller, Jr. Memorial Parkway. Grand Teton and Yellowstone national parks include some of the most topographically complex and climatologically heterogeneous protected areas in the conterminous U.S. (Tercek et al., 2012). Elevation ranges from 1600 m in the lowest portion of Yellowstone to >4000 m in the Teton Range (Fig. 1). Lower elevations vegetation consists of sagebrush and grasslands with coniferous forests at middle and upper elevations. Areas of higher soil moisture include deciduous trees, willows, grass-sedge meadows, and forbs. The climate is characterized by long, cold winters and brief, cool summers, with considerable spatial heterogeneity in annual temperatures, precipitation, and runoff (Ray et al., 2016). Snow provides the primary source of surface water that fills wetlands (Schook and Cooper, 2014). Wetlands of the study area vary in size, depth, and hydroperiod, and are most prominently influenced by local soil permeability (Elliot and Hektner, 2000). Isolated, palustrine wetlands are the predominant wetland type and constitute approximately 3% of the area of the two parks (Gould et al., 2012).

2.2. Study design and data collection

Our sampling frame and methods are described in detail elsewhere (see Gould et al., 2012; Ray et al., 2016). Briefly, after separating the two parks into 3370 catchments averaging approximately 200 ha in size, we selected a stratified random sample of catchments that contained wetlands. The goal of this original effort was to identify wetlands that could serve as breeding habitat for pond-breeding amphibians. Catchments were initially stratified based on amount of mapped wetland habitat described on U.S. Fish and Wildlife Service (USFWS) National Wetland Inventory (NWI) maps (Cowardin et al., 1979). We categorized catchments as 1) high quality, which contained >4 ha of permanent and semi-permanent wetlands and > 2 ha of seasonally flooded wetlands (n = 135 catchments), 2) medium quality, which contained a lesser amount of permanent and semi-permanent wetlands (>0 ha and < 4 ha) and at least 1 ha of seasonally flooded wetlands (n = 990 catchments), and low quality, which were overwhelmingly the most common in both parks (n = 2245 catchments) and contained limited amounts of permanent or seasonal wetlands.

Here, we constrained our analyses to just high and medium quality catchments since these are the most wetland-rich portions of the sample frame (Ray et al., 2016). Like other semi-arid wetlands, intact subsurface flow paths from permanent water (e.g., permanent lakes,

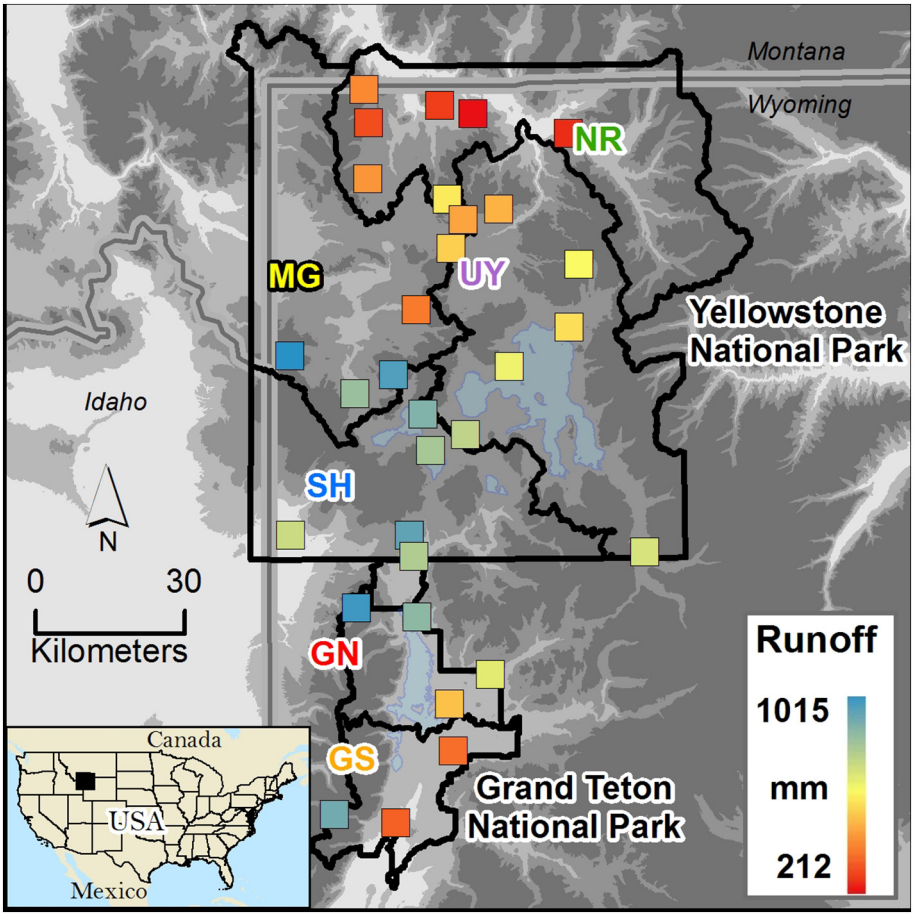

Fig. 1. Study area map showing locations of monitored catchments in Grand Teton and Yellowstone national parks. Inset map shows the location of national parks in the continental USA. Elevation contours are displayed with the lightest areas representing areas < 2000 m and darkest areas represent elevations > 2500 m. Hydrologic subbasins are labeled where GN = Grand Teton North subbasin, GS = Grand Teton South subbasin, MG = Madison-Gallatin subbasin, NR = Northern Range subbasin, SH = Snake-Henry's subbasin, and UY = Upper Yellowstone subbasin. To illustrate the spatial variation in April to June cumulative runoff across the region, we show multi-year, catchment-level means (using all wetlands in each catchment) for the 8-year time series.

Table 1
A priori candidate suite of models for analysis of the probability of wetland drying. Each model had the identical covariance structure (see Appendix A) of a random intercept for catchment and a random intercept for site to account for the hierarchical and repeated measures design.

Variable	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	M15	M16
Precip	X	X	X	X	X	X										
Temp				X	X	X	X	X	X							
Runoff										X	X	X				
ET													X	X	X	
% Water		X			X			X			X			X		
Depth			X			X			X			X			X	
Subbasin	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

Abbreviations: M = Model, Precip = April to June cumulative precipitation, Temp = April to June average air temperature, Runoff = April to June cumulative runoff, and ET = April to June cumulative actual evapotranspiration, % Water = proportion of mapped open water in each catchment, Depth = maximum wetland depth, and Subbasin = hydrologic subbasin.

rivers, and streams) may be important for maintaining wetland water levels across our sample frame (sensu Dwire et al., 2018; Euliss and Mushet, 1996). Therefore, we used the proportion of open water (% Water in Table 1) in each catchment, estimated using available U.S. Geological Survey National Hydrography Datasets (see nhd.usgs.gov), to explore the importance of permanent water to observed patterns in wetland drying.

Another type of stratification was applied to attain necessary spatial representation within the sample frame. Accordingly, monitored catchments were selected from six major hydrologic drainages (subbasins; Fig. 1). In the subbasin stratification, there was explicit recognition that major park drainages differ with respect to their parent geology, topography, elevation, climate patterns, and the existence or influence of large lakes or rivers. The resultant study design defined six subbasins within the sample frame (Grand Teton North, Grand Teton South, Madison-Gallatin, Northern Range, Snake-Henry's Fork, and Upper Yellowstone; Fig. 1).

Each year, from 2006 to 2013, we surveyed all wetlands identified on USFWS NWI maps or through on the ground observations that supported wetland characteristics and some expanse (e.g., >1 m^2) of open water. Because our research was linked to pond-breeding amphibian occupancy (see Gould et al., 2012), the stagnant (i.e., non-flowing) open water requirement was requisite for our monitoring. Accordingly, side-hill seep wetlands (lacking ponded water) or streams (containing flowing water) were not included in our analysis. At each wetland we documented the presence, associated size, and maximum depth of water in flooded wetlands and the absence of water in dry wetlands (see photo collages in Fig. 2 and Supplemental Fig. S1). We surveyed wetlands from mid-June through July, with lower elevation sites visited first and higher elevation sites visited later. Wetlands that were nearly dry (i.e., <2 cm of standing water and < 1 m^2 in size) were described as dry as those wetlands were likely to dry within days of our site visit. In total, we visited 331 wetland sites from 31 catchments across Grand Teton and Yellowstone national parks.

2.3. Meteorological variables

We used 1 km × 1 km Daymet gridded meteorological data (Thornton et al., 2014) in a water balance model (Thoma et al., 2015) to estimate evapotranspiration (in mm) and runoff (in mm) at all monitored wetlands. In brief, the water balance model incorporated gridded meteorological summaries in monthly time steps to quantify seasonal and annual variations in water availability for wetland filling (see Ray et al., 2016 for additional details on water balance approaches).

In its simplest form, on an annual basis with no change in soil moisture storage, the water balance equation is,

$$P = Ro + AET$$

where P is annual precipitation (in mm), Ro is runoff (in mm), and AET is actual evapotranspiration (in mm). Precipitation (P) is the sum of daily Daymet grid cell precipitation. Runoff (Ro) is surplus water input after soil water-holding capacity is satisfied, and in this model, includes downward infiltration plus lateral interflow and surface runoff. Actual evapotranspiration (AET) is water that returns to the atmosphere via transpiration and evaporation.

Late winter snowpacks and weather conditions of spring and early summer strongly influence the amount and persistence of surface water in shallow wetlands across Grand Teton and Yellowstone national parks (Corn, 2005; Ray et al., 2015; Schook and Cooper, 2014). Accordingly, we hypothesized that current year April to June summaries of four meteorological drivers (average air temperature, cumulative precipitation, cumulative actual evapotranspiration, and cumulative runoff) would have the greatest influence on wetland inundation and drying. Runoff estimates generated using a water balance approach explicitly incorporated soil drying from the previous summer and fall. And, runoff was generated in spring (April to June) only after soil moisture storage capacity was exceeded by the melting snowpack and augmented by spring rain. Further, we hypothesized that precipitation and actual evapotranspiration rates from April to June were most likely to affect wetland persistence (Ray et al., 2016). Finally, we recognized that air temperature effects on wetlands are complex but based on work by McMenamin et al., 2008 and others hypothesized that elevated air temperatures would be directly related to wetland drying.

2.4. Analytical methods

The goal of our analysis was to use generalized linear mixed models to explore the associations between annual wetland drying observations and meteorological drivers (temperature, precipitation, evapotranspiration, and runoff) through time and across multiple hydrologic subbasins within Grand Teton and Yellowstone national parks. Generalized linear models allow for modeling a binary response variable, in our case whether the wetland was dry or not, as a function of explanatory variables (e.g., evapotranspiration), similar to linear regression models. A generalized linear *mixed* model allows for a more complicated error or covariance structure to reflect different components of variation. We conducted all statistical analyses in R (R Core Team, 2015). Generalized linear mixed models were estimated using the glmer function in the lme4 package (Bates et al., 2014).

Our general approach was to first find the appropriate covariance structure (random effects; see Appendix A). We developed the covariance structure of the model to reflect that sites were nested within catchments and sites were surveyed repeatedly over time. The random selection of catchments supported inference to the wider population of wetland-rich (medium and high quality) catchments within Grand Teton and Yellowstone national parks. Similarly, a site-level random effect accounted for the repeated measurements of sites across years, since measurements taken at a site will likely be more similar among years.

An appropriate covariance model is essential to obtain valid inferences for the effects of meteorological variables on wetland drying (Verbeke and Molenberghs, 2000; Cheng et al., 2010). Therefore, we examined possible random effects or covariance structures with a

Fig. 2. Photographs of annual wetland visits to an isolated wetland on the Blacktail Plateau in Yellowstone's Northern Range. This shallow wetland (max depth < 1 m in years with water) was dry during early July sampling visits in 2007, 2010, and 2013.

preliminary mean structure prior to investigating the associations between wetland drying and meteorological variables. The preliminary mean structure included fixed effects for a meteorological variable (e.g., April to June precipitation) and hydrologic subbasin (additional details provided in Appendix A). The evaluation of the covariance structure depended on a rich understanding of wetland dynamics and drivers of wetland change, as well as, statistical criteria. With respect to the latter, including too few random components could have resulted in underfitting bias (Cheng et al., 2010). Thus, we began with a maximum model in terms of the covariance structure, allowing for random intercepts and slopes (i.e., varying linear yearly trends) at the site- and catchment-level (e.g., modifying the trend model proposed by Piepho and Ogutu, 2002) to account for the additional complexity in our design. However, we also recognized there may be insufficient observations per site to estimate this complex covariance structure. Fitting too complex a covariance structure for the available data can result in the mixed model algorithm failing to converge, which manifests in random effect variance component estimates of 0 or estimated correlation among random effects close to 1 (Bates et al., 2015). Consequently, we explored two reduced covariance structures: one that only included random intercepts and slopes for sites (i.e., varying linear yearly trends by site) and a random intercept for each catchment; and another that only allowed for a random intercept for each site and a random intercept for each catchment. We evaluated the sensitivity of the selection of covariance structure given the preliminary mean structure.

Generally, the estimated correlations between intercepts and slopes were high across all meteorological variables and were suggestive of an overparameterized model. When a random intercept and slope were included at the site-level, the random intercept estimated at the catchment-level had a standard deviation of 0. These findings are also indicative of an overfitted model (Bates et al., 2015; Matuschek et al., 2017) and point to an optimal covariance structure for the wetland drying time series that included a random intercept for catchment and a random intercept for site (see Appendix A for additional details). Once the appropriate set of random effects was determined, we applied model selection criteria to a set of a priori models with different sets of explanatory variables (Table 1). To improve model convergence, we first centered and scaled meteorological variables.

Fifteen a priori models with different fixed effects were parameterized to reflect competing hypotheses regarding whether wetland drying documented from 2006 to 2013 was associated with meteorological, site- and catchment-level variables (Table 1). An overall intercept and intercept adjustments for each subbasin were included as fixed effects in all a priori models. We compared results of the a priori model set to a model with no meteorological variable (only subbasin and an intercept as fixed effects, M16 in Table 1).

We used Akaike information criteria (Burnham and Anderson, 2002) and Bayesian information criteria (Schwarz, 1978) to rank models with varying meteorological variables. Although Bayesian information criteria (BIC) has generally been described as a better performer for small sample sizes (Gurka, 2006), our work included a relatively large number of observations ($n = 2304$) from over 330 sites. The majority of sites had 7 observations between the years 2006 to 2013; however, for the purposes of inclusion all sites had to have a minimum of 2 years of observations. We present results from both Akaike information criteria (AIC) and BIC and note that models where the difference in score (ΔAIC and ΔBIC) fell between 2 and 7 had some support (Burnham et al., 2011). We calculated the adjusted R^2 (Nakagawa and Schielzeth, 2013) as an indicator of goodness of fit for each model because AIC and BIC are only relative measures of the information content of different models and do not actually assess how well the suite of candidate models fit the observed data (Burnham and Anderson, 2002).

Lastly, we used our highest ranking model to explore how variations in meteorological variables influenced the probability of drying across

subbasins. We estimated marginal means to clearly distinguish the effect of varying runoff on wetland drying for each subbasin and to make pairwise comparisons among subbasins. Meteorological variables differed dramatically through time and across our region with higher elevation wetlands and catchments representing outliers for April to June cumulative runoff. To address this issue, we explored three levels for each meteorological covariate. For runoff, we used a range of runoff estimates (225 to 525 mm) that represented the median among-year runoff estimates for the lowest runoff catchments to intermediate runoff catchments.

Unexpectedly, we found little utility for models that included wetland depth (Table 1). All models including wetland depth were poorly estimated. These models had large estimated coefficients ($|\beta'| > 10$) and standard errors (SE (β') > 100) for wetland depth, implying that the wetland drying response was almost completely separated by the wetland depth variable. With few exceptions, wetlands that were documented as dry were shallow, with maximum depths <1 m when inundated. Approximately 90% of the 139 wetlands documented as dry at least once during the 8-year time series had maximum depths of <1 m when flooded. Because wetland depth was so strongly correlated with the drying response, model selection results excluded models that included wetland depth.

3. Results

Between 2006 and 2013, we visited 331 wetland sites from 31 catchments representing a total of 2304 site-visits across Grand Teton and Yellowstone national parks. Sites included in this analysis were visited in multiple years, but not all sites were visited each year (see Fig. 2 for annual photographic summaries of a single wetland in Yellowstone's Northern Range). In 2008, 2009, and 2011 only 5 to 6% of wetland sites were dry during our mid-June to late-July field visits. In contrast, >30% of visited sites were dry across both parks in 2007 (see Table 2).

Regionally, conditions were more favorable for retaining water in 2011 when the average April to June temperatures in our time series combined with high levels of precipitation and a large snowpack. In contrast, 2007 was the warmest April to June period in our time series and precipitation and snowmelt runoff levels were a fraction of other years (Table 2 and Fig. 3). Overall, wetlands from the Northern Range and Grand Teton South subbasins received the lowest levels of snowmelt driven runoff (2006 to 2013 among-year global median of 308 mm [NR] and 394 mm [GS]). Wetlands in the Grand Teton North and Snake-Henry's subbasins consistently received the highest levels of runoff and the among-year global medians were 579 mm [GN] and 673 mm [SH], respectively (see Fig. 1 and Supplemental Table S1). Even within the same catchment or subbasin, individual wetlands showed varying responses to wetland drying (see photographic examples showing among year changes from 2 wetlands within Yellowstone's Northern Range subbasin; Fig. 2 and Supplemental Fig. S1).

Table 2
Regional April to June summaries (mean ± 1 SD) of meteorological variables for each year and the associated percentage of surveyed wetland sites across both parks that were dry by a mid-June to late-July field visit.

Year	ET (mm)	Precip (mm)	Runoff (mm)	Temp (°C)	% wetlands dry
2006	132 ± 7	172 ± 45	552 ± 215	7.2 ± 1.0	13
2007	130 ± 7	110 ± 19	366 ± 157	7.4 ± 0.9	32
2008	93 ± 5	221 ± 52	673 ± 191	4.4 ± 0.8	5
2009	117 ± 16	309 ± 49	592 ± 175	5.6 ± 1.1	6
2010	99 ± 18	307 ± 67	455 ± 158	4.1 ± 1.0	13
2011	91 ± 15	355 ± 87	785 ± 237	3.7 ± 1.0	6
2012	124 ± 5	180 ± 41	508 ± 171	6.5 ± 1.1	24
2013	102 ± 13	149 ± 28	405 ± 154	5.5 ± 1.1	27

Abbreviations: Precip = April to June cumulative precipitation, Temp = April to June average air temperature, Runoff = April to June cumulative runoff, and ET = April to June cumulative actual evapotranspiration, and % wetlands dry = percentage of monitored wetlands that were dry during annual mid-summer visits.

The optimal covariance structure for the wetland drying data for our 8-year time series included a random intercept for catchment and a random intercept for site. There was no support for a structure that included a random slope for year at the site and catchment levels. This suggests that the probability of drying varies spatially among sites and catchments. The data available, however, did not support additional model complexity that allows for the relationship (i.e., random slope estimates) between runoff and probability of drying to vary by site and catchment (see Appendix A). Thus, we proceeded with a model that included only random intercepts at both the site- and catchment-level when evaluating the associations between wetland drying and meteorological variables of interest.

We found strong evidence that meteorological drivers were associated with wetland drying patterns. All models containing meteorological variables explained more variation in the drying dataset than the model that attempted to describe variation in wetland drying without meteorological variables (M16; Table 3). The model with cumulative April to June runoff had the most support and a marginal, adjusted $R^2 = 0.228$ and a conditional, adjusted $R^2 = 0.824$ and runoff and drying were inversely related. The second model ($\Delta AIC = 1.49$, $\Delta BIC = 7.23$) included the proportion of water within the catchment but offered no real explanatory power relative to our highest ranked, runoff only model (Table 3).

Declines in runoff were associated with increased drying probabilities across all subbasins in Grand Teton and Yellowstone national parks (Supplemental Fig. S2). Using the model structure of Eq. (3) in Appendix A, we summarized changes in drying probability as a function of runoff. The Snake-Henry's subbasin (Fig. 1) shows a fivefold increase in drying probability when runoff declines from 525 mm to 225 mm (Table 4). Within the Madison-Gallatin and Upper Yellowstone subbasins, the probability of wetland drying is 0.342 (95% CI = 0.099, 0.711) and 0.246 (95% CI = 0.083, 0.540) at an estimated runoff level of 225 mm. For the Northern Range and Grand Teton North and South subbasins, the probability of wetland drying never exceeded 0.100 even at the lowest runoff levels (Table 4).

When the probability of wetland drying was compared across subbassins the differing responses to variations in runoff became even more apparent. The odds of wetland drying in the Snake-Henry's and Madison-Gallatin subbasins were 54.5 (95% CI from 8.6 to 348.2) and 8.7 (95% CI from 1.4 to 56.0) times the odds of wetlands drying in Yellowstone's Northern Range. The odds of wetlands drying in Grand Teton North (1.7 times odds of Northern Range; 95% CI from 0.2 to 13.2) and Grand Teton South (1.6 times odds of Northern Range; 95% CI from 0.2 to 13.9) subbasins were similar to those of the Northern Range. The Northern Range subbasin serves as an interesting benchmark because it receives just half the levels of runoff used to fill wetlands in Snake Henry's and Grand Teton North subbasins and considerably lower runoff levels than Madison-Gallatin and Upper Yellowstone subbasins (Table S1). The negative association between cumulative April to June runoff and the probability of wetland drying is summarized for all subbasins in Fig. 4.

4. Discussion

There is mounting evidence that wetlands are susceptible to changes in climate (Johnson and Poiani, 2016; Klein et al., 2005; Lee et al., 2015; Ryan et al., 2014; Sofaer et al., 2016; Zhang et al., 2016). In Grand Teton and Yellowstone national parks, a higher percentage of surveyed wetlands are dry in years characterized by lower spring and early summer runoff. While wetland drying is widespread across both parks, we found considerable support that the probability of wetland drying varied most among subbasins. Subbasin or sub-regional differences in wetland drying have been documented elsewhere (see Klein et al., 2005; Sofaer et al., 2016). Incongruous, subbasin hydrologic responses to

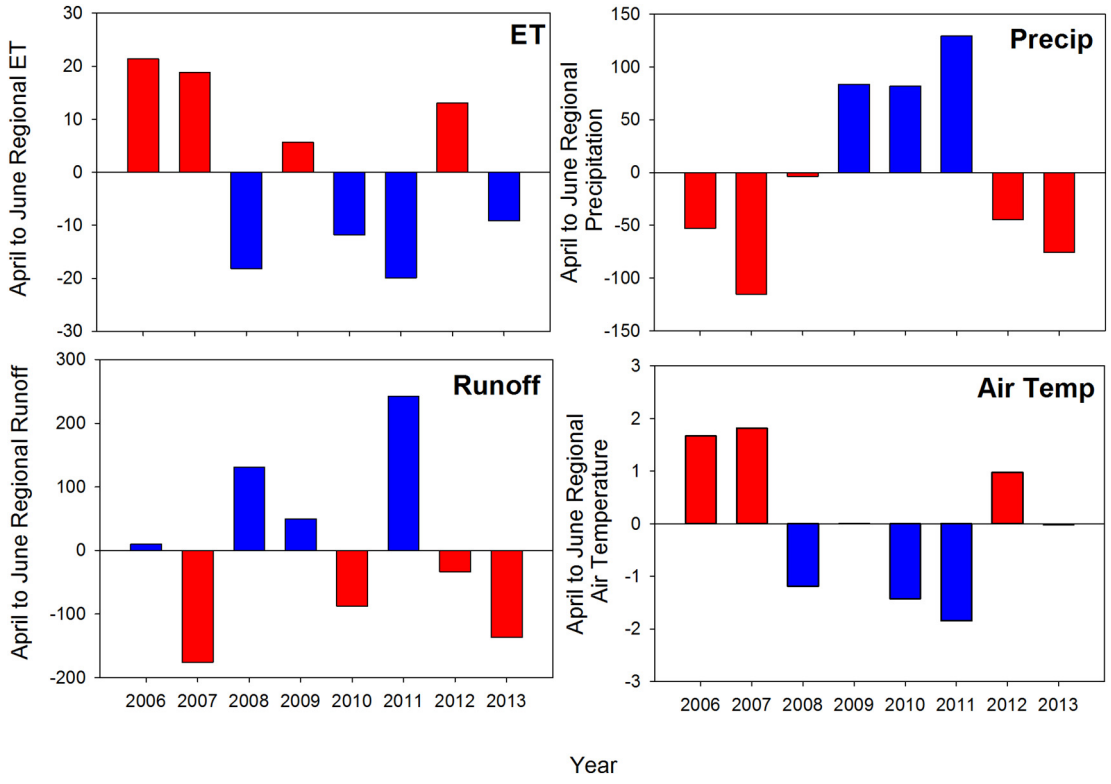

Fig. 3. Regional average meteorological covariates (April to June cumulative actual evapotranspiration, April to June cumulative precipitation, and April to June cumulative runoff and average April to June air temperature) relative to the 8-year average. Positive values indicate annual regional averages exceeded the 8-year average. Negative values indicate annual regional averages were below the 8-year average.

recent meteorological variations are not unexpected, particularly in topographically and climatologically complex regions such as ours (Al-Chokhachy et al., 2017). Documenting the varying responses of wetlands from individual subbasins to meteorological change is a necessary first step to identifying subbasins or sub-regions where wetland drying will become more pronounced and contemplating how future climatic change may alter the distribution of wetland dependent taxa (Ryan et al., 2014).

Table 3
Adjusted R^2, Δ AIC and Δ BIC for models of wetland drying from the a priori set (Table 1). Each model is a generalized linear mixed model with regression coefficients for an intercept, subbasin, meteorological covariate, and the proportion of catchment area in water. All models had an identical covariance structure with a random intercept for catchment and a random intercept for site (covariance structure as in eq. 3 from Appendix A). The marginal adjusted R^2 can be interpreted as the variance explained by fixed factors, while the conditional R^2 can be interpreted as the variance explained by both fixed and random factors.

Model	Meteorological driver	Prop. water	Δ AIC	ΔBIC	Adjusted R^2	
					Marginal	Conditional
M10	Runoff		0.00	0.00	0.23	0.82
M11	Runoff	X	1.49	7.23	0.22	0.82
M4	Precip, Temp		37.63	43.37	0.15	0.75
M1	Precip		38.58	38.58	0.15	0.75
M5	Precip, Temp	X	39.37	50.85	0.15	0.75
M2	Precip	X	40.07	45.81	0.15	0.75
M7	Temp		107.42	107.42	0.11	0.70
M8	Temp	X	109.41	115.16	0.11	0.70
M13	ET		144.00	144.00	0.08	0.67
M14	ET	X	145.69	151.43	0.08	0.67
M16			222.07	216.33	0.03	0.61

Abbreviations: Precip = April to June cumulative precipitation, Temp = April to June average air temperature, Runoff = April to June cumulative runoff, and ET = April to June cumulative actual evapotranspiration, and Prop. water = proportion of mapped open water in catchment.

Yellowstone's Northern Range has been the topic of previous studies documenting wetland change and summarizing the biological impacts of drying (see McMenamin et al., 2008; Schook and Cooper, 2014). Although this study further demonstrates that Northern Range wetlands have and are likely to respond to future changes in runoff, and to a lesser extent, precipitation, and temperature, other subbasins in Yellowstone and Grand Teton national parks that currently receive considerably more runoff show an even greater probability of drying with a reduction in runoff relative to current levels. For example, the odds of wetland drying in the Snake-Henry's and Madison-Gallatin subbasins was >50 and nearly 10 times the odds of wetland drying in the Northern Range given a comparable future runoff level. Additionally, the odds of wetlands drying in both Grand Teton National Park subbasins were comparable to Yellowstone's Northern Range.

While individual wetlands may be more or less resistant to future change, we found a strong relationship between runoff and increased probability of wetland drying. And, although these models were explanatory and not predictive in nature, this strong relationship suggests an overall reduction in the total number of wetlands across both parks if predicted changes to regional snowpacks and corresponding declines in runoff are realized (see Pederson et al., 2011). This is consistent with work elsewhere and further corroborates claims that wetlands even within highly protected landscapes are likely to respond to future climatic change. In Olympic, Mountain Rainier, and North Cascades national parks, a dramatic decline in wetland area is expected by 2080. Specifically, dramatic losses are expected for shallow, ephemeral wetlands and hydrologic regime transitions from permanent and semi-permanent to ephemeral are anticipated (Lee et al., 2015). Although climate interacts with other disturbances affecting wetlands in the Prairie Pothole Region, both wetland area and abundance changes have also been linked to recent and long-term climatic change (Liu and Schwartz, 2012; McIntyre et al., 2014; Sorenson et al., 1998). Climate projections indicate further wetland declines across the Prairie Pothole Region; however an unbalanced pattern of changes is expected with

Table 4
Estimated mean probability of wetland drying given specified, cumulative April-to-June runoff (in mm). Estimates provide population means and t-based confidence intervals by subbasin, and were derived from fitted model M10 (Table 1) including fixed effects for intercept, subbasin, and runoff, and random intercepts for catchment and nested site within catchment.

Subbasin	Runoff = 225 mm		Runoff = 375 mm		Runoff = 525 mm	
	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
GN	0.091	(0.017, 0.367)	0.023	(0.004, 0.122)	0.005	(0.001, 0.033)
GS	0.085	(0.012, 0.411)	0.021	(0.003, 0.145)	0.005	(0.001, 0.041)
MG	0.342	(0.099, 0.711)	0.108	(0.025, 0.366)	0.028	(0.006, 0.124)
NR	0.056	(0.013, 0.215)	0.014	(0.003, 0.063)	0.003	(0.001, 0.017)
SH	0.764	(0.444, 0.929)	0.432	(0.164, 0.747)	0.151	(0.044, 0.408)
UY	0.246	(0.083, 0.54)	0.071	(0.021, 0.217)	0.018	(0.005, 0.064)

Abbreviations: GN = Grand Teton North subbasin, GS = Grand Teton South subbasin, MG = Madison-Gallatin subbasin, NR = Northern Range subbasin, SH = Snake-Henry's subbasin, and UY = Upper Yellowstone subbasin, Runoff = April to June cumulative runoff.

some sub-regions experiencing more severe declines (Sofaer et al., 2016). Lastly, in Alaska's Kenai Lowlands, wetland drying over the last half century was detected in 80% of the surveyed sites; wetland drying was associated with decreased precipitation levels and increased air temperatures (Klein et al., 2005).

In the western U.S., the hydroperiods of larger, deeper, hydrologically connected wetlands are less sensitive to annual variations in meteorological conditions and are able to withstand extended periods of drought better than shallow, isolated wetlands (Hossack et al., 2013; Klein et al., 2005; Lee et al., 2015). Within Yellowstone National Park, deeper groundwater or surface water-connected wetlands with relatively stable water levels have persisted despite widespread water declines over the last several decades (Schook and Cooper, 2014). From our monitoring in Yellowstone and Grand Teton national parks we also documented the overwhelming influence of wetland depth. Here, we determined that with few exceptions wetlands that were observed as dry during the 8-year time series also had a maximum depth (when inundated) that was <1 m. Although wetland depth was strongly coupled with drying, many shallow wetlands (depth < 1 m) contained standing water during all site visits. Surprisingly, our estimate of local surface water abundance, a static proxy for local to regional water abundance (Sophocleous, 2002), offered no additional strength to models containing meteorological variables alone. These results contrast with glacier meltwater dependent wetlands elsewhere, where changes in wetland area were associated with watershed size, recent precipitation, and percentage of watershed in snow or glacier covered surfaces

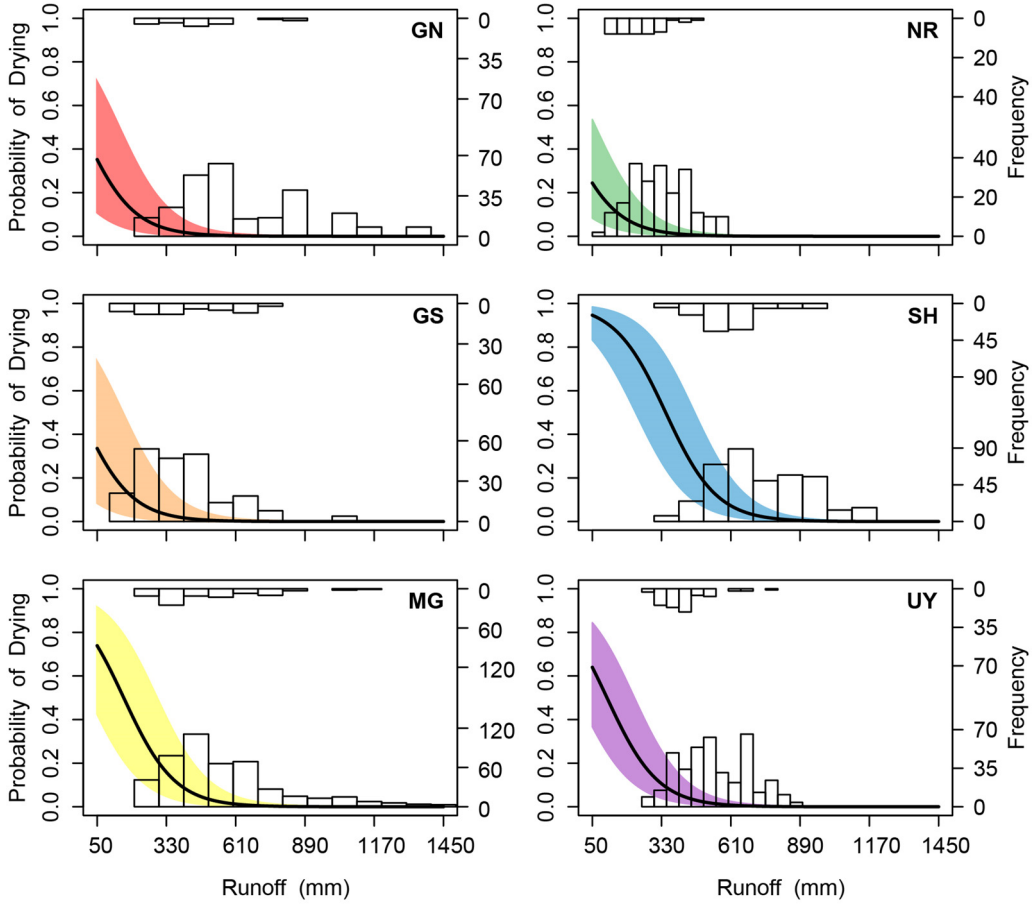

Fig. 4. Probability of wetland drying is negatively associated with cumulative April-to-June runoff (mm) for each subbasin. Histograms correspond to counts of individual wetland sites that were dry (y = 1; top axis) or wet (y = 0; bottom axis) for associated runoff level across all years (2006 to 2013). The solid line shows the estimated generalized mixed model of probability of wetland drying as a function of runoff at the maximum likelihood estimates of model coefficients (Model M10 in Table 1). Confidence intervals (colors) are point-wise, t-based, 90% intervals. Subbasin abbreviations are as follows: GN = Grand Teton North, GS = Grand Teton South, MG = Madison-Gallatin, NR = Northern Range, SH = Snake-Henry's, and UY = Upper Yellowstone.

(Dangles et al., 2017). While accounting for the abundance of local water, we did not evaluate other wetland characters such as substrate type or wetland shape that have contributed significantly to wetland persistence even during periods of drought (Dangles et al., 2017; Klein et al., 2005).

Across Grand Teton and Yellowstone national parks, variations in snow-melt driven runoff were most strongly related with annual variations in the proportion of dry wetlands. Across this and other high elevation regions, snowmelt runoff serves as the primary source of moisture filling wetlands (Corn, 2005; Ryan et al., 2014; Zhang et al., 2016). In the Northern Rocky Mountains, a reduction in snowpack volumes and shift towards earlier spring runoff have been documented. Early runoff patterns (Pederson et al., 2011) correspond with rapidly increasing spring temperatures (Sepulveda et al., 2015) and have contributed to earlier onset of peak river flows (Al-Chokhachy et al., 2017). In other snow-dominated landscapes, wetlands are experiencing earlier drawdowns, accelerated recession rates, and lower minimum water levels as snowpack declines initiate earlier runoff (Blanken, 2014; Lee et al., 2015). While our observations do not allow us to characterize shifting wetland hydroperiods, our annual visits to >300 wetlands distributed across Yellowstone and Grand Teton national parks demonstrate the spatiotemporal patterns of mid-summer drying are largely driven by variations in spring and early summer runoff. In 2007, the year with the lowest region-wide runoff estimates in our time series, an estimated 32% of wetlands visited across both parks were dry by mid-summer. In contrast, runoff estimates in 2011 were the highest in our time series and just one sixth of the wetlands dry in 2007 were dry in 2011. Across the region, there was a 2-fold difference in cumulative April to June runoff comparing 2007 and 2011. Although among year variation in runoff was high at the regional scale; among year variations were much higher at catchment and subbasin scales (see Supplemental Table S1 for catchment- and subbasin-level summaries) and exhibited no clear patterns with elevation.

Here we offer additional evidence of the utility of water balance approaches to model past wetland dynamics over large areas and through time. Water-balance runoff estimates used to explain wetland flooding dynamics across both parks incorporated the carry-over effects of summer and fall evapotranspiration, snowpack water content, and spring and early summer rain. Using a similar approach, Lee et al. (2015) showed that intermediate and deep soil moisture estimates were strongly correlated with observed water levels in montane wetlands. In studies of wetlands across the Prairie Pothole Region, Liu and Schwartz (2012) integrated precipitation and evapotranspiration into a single index to explain two decades of variation in wetland area and abundance. Sofaer et al. (2016) used a comparable index with a one-year lag to best explain interannual patterns of wetland density across the Prairie Pothole Region. A common feature of these studies is that they provide a monthly, seasonal, or annual accounting of wetland hydrologic inputs and losses (Bardecki, 1991; Liu and Schwartz, 2011). These approaches also account for processes that interact across seasons by accounting for summer and fall evapotranspiration, winter snowpack accumulation, and spring melt. In this way, the proportion of precipitation that fills wetlands, the timing of its availability, and the dependence on antecedent drying from earlier time periods are all considered explicitly to produce estimates of runoff and other important hydrologic drivers (Thoma et al., 2015).

Identifying the spatiotemporal drivers of wetland hydrologic change is critical to conceiving and implementing systematic wetland conservation plans across large heterogeneous regions and fundamental to the execution of targeted conservation strategies (Liu and Schwartz, 2012; Ryan et al., 2014). In Yellowstone and Grand Teton national parks annual observations from hundreds of wetlands has greatly increased our understanding of the climate-driven dynamics of individual wetland change. The results of this analysis also offer an understanding of the subbasin-level variations in drying probabilities and show that drying was most strongly associated with seasonal runoff estimates. This latter finding distinguishes the current effort from previous studies of wetland change across Yellowstone's Northern Range which found wetland drying was associated increased warming and longer-term periods of drought (McMenamin et al., 2008; Schook and Cooper, 2014). Our inclusion of shallow and deep wetlands from multiple subbasins suggests that deep wetlands have a low probability of drying, but even equally shallow wetlands within a regional setting are likely to exhibit varying sensitivities to changes in runoff and other meteorological drivers. These differences in sensitivity may reflect unaccounted for annual differences in soil water storage, groundwater connectivity, or wetland shape, or may reflect other unmodeled factors (Lee et al., 2015; Zhang et al., 2016) associated with our annual surveys. Regardless, understanding and quantifying sub-regional differences in wetland drying allows land managers to anticipate and potentially mitigate consequences of future changes and to develop systematic conservation plans (Wilson et al., 2005) for the long-term conservation of wetlands and the growing list of sensitive species dependent on them.

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